REVIEW

How Animals Move: An Integrative View

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Recent advances in integrative studies of locomotion have revealed several general principles. Energy storage and exchange mechanisms discovered in walking and running bipeds apply to multilegged locomotion and even to flying and swimming. Nonpropulsive lateral forces can be sizable, but they may benefit stability, maneuverability, or other criteria that become apparent in natural environments. Locomotor control systems combine rapid mechanical preflexes with multimodal sensory feedback and feedforward commands. Muscles have a surprising variety of functions in locomotion, serving as motors, brakes, springs, and struts. Integrative approaches reveal not only how each component within a locomotor system operates but how they function as a collective whole.

Locomotion, movement through the environment, is the behavior that most dictates the morphology and physiology of animals. Evolutionary pressures for efficient, rapid, adjustable, or just plain reliable movement often push the envelope of organism design. Biologists have long been attracted to locomotor extremes because they provide especially clear examples from which to determine structure-function relations. It is not a coincidence, for example, that David Keilin first discovered cytochromes within insect flight muscle, a tissue that exhibits the highest known metabolic rate, or that J. Z. Young discovered a giant axon in a squid, an animal capable of rapid escape responses through jet propulsion. Other fundamental discoveries regarding central pattern generators, visual processing, skeletal remodeling, and many other important physiological phenomena originated from studies of locomotion. Locomotion is not, however, the simple net outcome of isolated specializations in individual cells and tissues. Although it is possible to deconstruct the mechanics of locomotion into a simple cascade—brain activates muscles, muscles move skeleton, skeleton performs work on external world—such a unidirectional framework fails to incorporate essential dynamic properties that emerge from feedback operating between and within levels. One key challenge in the study of locomotion is to determine how each individual component within a locomotor system operates, while at the same time discovering how they function collectively as an integrated whole.

An integrative approach to locomotion focuses on the interactions between the muscular, skeletal, nervous, respiratory, and circulatory systems. These systems possess functional properties that emerge only when they interact with each other and the environment. Frequently, model organisms are chosen because they perform some function exceptionally well. When performance is exaggerated, structure-function relations become more obvious. From studies on specialized animals, we can extrapolate to other systems in which the properties of interest are not present in the extreme, but in which the principles of function are fundamentally the same. Effective comparison demands data on many model systems. Fortunately, the experimental and computational tool kit available to study locomotion has expanded explosively in recent years (*1*), making comparisons possible among a large variety of animals, both in the lab and in nature.

As we review recent advances in the integrative and comparative study of animal locomotion, four themes emerge. First, the spatiotemporal dynamics of locomotion are complicated but understandable on the basis of a few common principles, including common mechanisms of energy exchange and the use of force for propulsion, stability, and maneuverability. Second, the locomotory performance of animals in natural habitats reflects trade-offs between different ecologically important aspects of behavior and is affected by the physical properties of the environment. Third, the control of locomotion is not a linear cascade, but a distributed organization requiring both feedforward motor patterns and neural and mechanical feedback. Fourth, muscles perform many different functions in locomotion, a view expanded by the integration of muscle physiology with whole-animal mechanics. These emergent themes are by no means an exhaustive list (*2, 3*), and they leave room for future reviews. In particular, we note that important advances in energetics, exercise physiology, molecular biomechanics, biophysical ecology, and many aspects of neurobiology are beyond the scope of this review.

Forcing the Issue

At its most fundamental level, locomotion is deceptively simple. An organism exerts a force on the external environment and, through Newton's laws, accelerates in the opposite direction. Yet, studies of walking, running, swimming, and flying indicate that the spatial and temporal dynamics of force application are not as simple as they might first appear. From whale sperm to sperm whales, locomotion is almost always produced by appendages that oscillate or by bodies that undulate, pulse, or undergo peristaltic waves. As a consequence, although an animal may appear to move forward at a steady speed, the forces it exerts on the environment are anything but constant.

As a general illustration of the complexities of the temporal and spatial variation of locomotor forces, we show examples from a diverse assortment of animals in Fig. 1. First, consider legged locomotion on land, where each leg pushes against the ground, producing an equal and opposite ground reaction force (Fig. 1A). Two basic mechanisms have been proposed to explain the different patterns of time-variant forces measured during walking and running (Fig. 1B) (*4–6*). When animals walk, the body vaults up and over each stiff leg in an arc, analogous to an inverted pendulum (Fig. 1B). Kinetic energy in the first half of the stance phase is transformed into gravitational potential energy, which is partially recovered as the animal's body falls forward and downward in the second half of the stance phase (*4, 7, 8*). To travel faster, legged animals change to running gaits that are analogous to bouncing on a pogo stick (Fig. 1B) (*4, 7, 9–12*). As a leg strikes the ground in a running gait, kinetic and gravitational potential energy is temporarily stored as elastic strain energy in muscles, tendons, and ligaments and then is nearly all recovered during the propulsive second half of the stance phase. Remarkably, these basic mechanisms of energy conservation have been demonstrated in a wide variety of animals that differ in leg number, posture, body shape, body mass, or skeleton type (*13–15*), including humans, kangaroos, dogs, lizards, crabs, and cockroaches (*4, 16–18*).

Surprisingly, time-variant forces and energy exchange in the lateral direction could be equally important. The legs of sprawled-posture animals such as insects (Fig. 1C) (*18–20*), crabs (*14*), crayfish (*21–23*), spiders (*24*), and geckos (*17*) generate substantial lateral forces while in contact with the ground. The time course of these lateral forces is consistent with the hypothesis that elastic energy storage and recovery may occur within the horizontal plane (*25, 26*), orthogonal to the direction of motion. In addition,

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lateral forces may enhance both the passive stability and active maneuverability of locomotion. By pushing laterally, legs create a more robust gait that can be passively self-stabilizing as the animal changes speed, moves over uneven ground, or is knocked askew by uneven terrain, a gust of wind, or a would-be predator (*27*). Species with sprawled postures can actively alter course by changing the orientation of forces generated by a single leg (*23, 28*).

Whereas the legs of a runner push against a solid substrate, the appendages and body of swimmers and fliers push against fluids, which distort and swirl to form a complex wake (Fig. 1, D and E). As an animal moves through a fluid, it creates vorticity, a circular flow of motion that represents the momentum imparted by the animal to the fluid. Although vorticity may be distributed continuously throughout a fluid, an important advance in the study of locomotion came with the recognition that the wakes of swimming and flying animals are often packaged into a series of discrete or linked vortex rings (Fig. 1D) (*29–33*). It is not possible to directly measure the forces generated by an animal; however, it is possible to visualize the formation of its vortex wake and, from such data, reconstruct the spatial and temporal dynamics of force generation. Such attempts have been greatly advanced through the development of digital particle image velocimetry (*34*), which employs a spatial cross-correlation technique to resolve the local velocity within a slice of fluid (Fig. 1E). Although the geometry of such wakes is complex and differs among species or within an individual, depending on swimming speed or the fins used (*33, 35–38*),

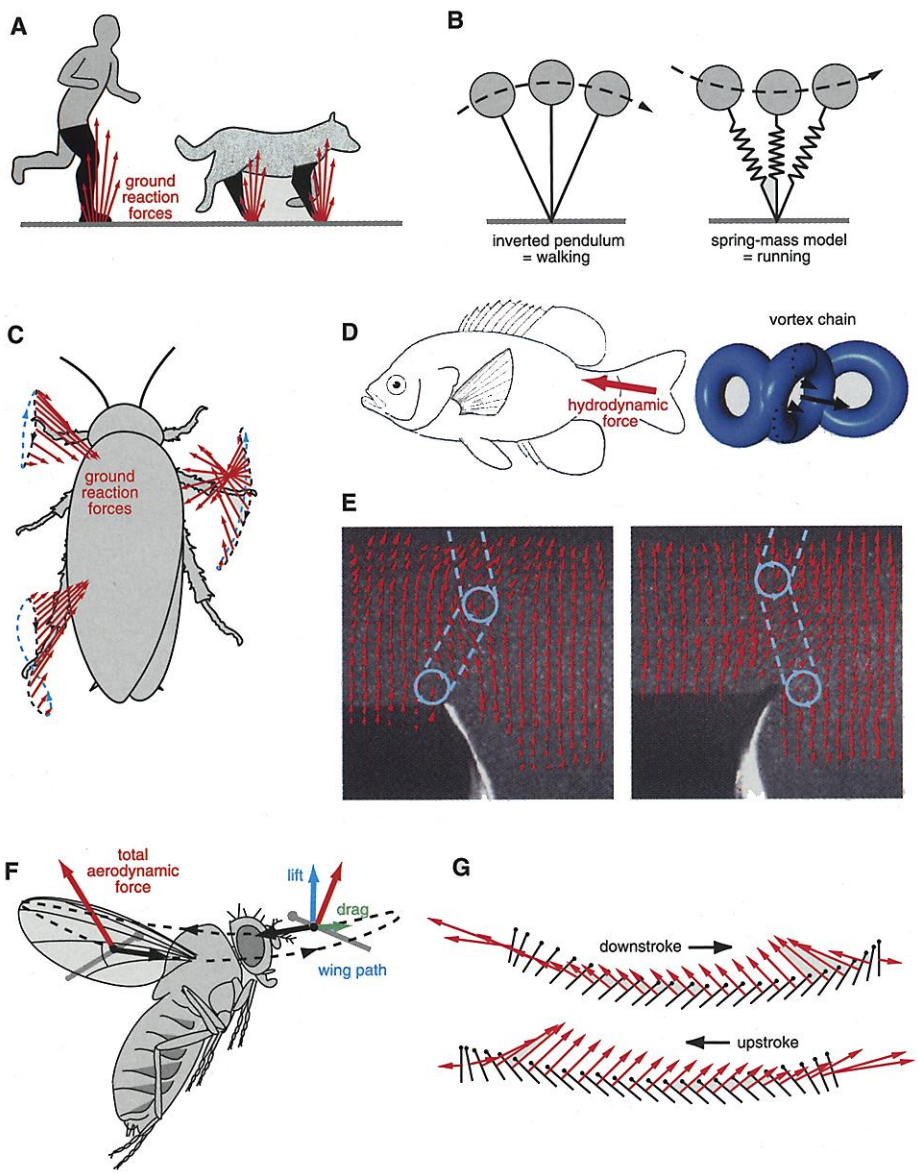

Fig. 1. Forces exerted by moving animals vary in space and time. (**A**) Ground reaction force vectors (shown in red) for a running human and trotting dog are plotted at equal time intervals throughout the stance phase. At each instant, the resultant vector points through the hip or shoulder of each leg, minimizing the torque at each joint. An initial braking phase is followed by a propulsive phase. (**B**) Two basic models for legged locomotion. In a walking animal, the center of mass vaults over a rigid leg, analogous to an inverted pendulum. At mid stance, the center of mass reaches its highest point. Like a pendulum, the kinetic and gravitational potential energies of the body are exchanged cyclically. In a running animal, the leg acts as a spring, compressing during the braking phase and recoiling during the propulsive phase. At mid stance, the center of mass reaches its lowest point. Like a simple spring-mass system, the kinetic and gravitational potential energies are stored as elastic energy during the braking phase and recovered during the propulsive phase. (**C**) In a running cockroach, hind-leg ground reaction forces propel the animal forward, whereas each foreleg ground reaction force pushes backward, counter to the animal's movement. The middle-leg ground reaction force begins by pushing backward but then pushes forward at the end of the stance phase. In addition to these fluctuating fore-aft forces, all legs act to push the body toward the midline. Black (stance phase) and blue (swing phase) dotted lines indicate the path of the distal end of each leg relative to the whole-body center of mass. Data are from (*120*). (**D**) Reconstruction of vortex wake behind a swimming fish (*121*). As the tail sweeps back and forth, it creates a series of alternating vortices. Each stroke of the fin creates a single donut-shaped vortex that is linked to the vortices of previous strokes. Each vortex represents the momentum imparted to the water by the fish's body and tail. By quantifying the water velocity induced by the shed vortex, it is possible to reconstruct the time-averaged hydrodynamic force acting on the fish. Black arrows indicate the velocity of water through the vortex ring. (**E**) Digital particle image velocimetry data for the wake behind the tail of a swimming bluegill as viewed from above (*121*). The head of the fish is oriented toward the bottom of the page. The two images indicate the fluid velocity near the beginning and end of one stroke. Raw data such as these can be used to reconstruct a vortex wake like that shown in (D). Each sweep of the tail fin sheds a pair of counterrotating vortices (shown in blue) that induce a flow outward and rearward. Red arrows indicate the water velocity. (**F**) Aerodynamic forces created by a fruit fly wing during hovering flight measured on a dynamically scaled model insect [adapted from (*51*)]. The wing of a hovering insect typically flaps back and forth at a high angle of attack during each stroke. The wing path is shown with a black dotted line. Black arrows indicate wing motion. Between strokes, the wing rapidly rotates so that the dorsal surface faces up during the downstroke and the ventral portion faces up during the upstroke. The total aerodynamic force (red) may be decomposed into lift (blue) and drag (green) components. (**G**) Diagram of wing motion indicating magnitude and orientation of the total aerodynamic force vector (red) generated throughout the stroke. Black lines indicate instantaneous position of the wing at temporally equidistant points during each stroke. Small circles indicate the leading edge of the wing. Time moves left to right during downstroke and right to left during upstroke.

one conclusion is clear: The magnitude and direction of the forces generated by the fish change over time and the fish generates a substantial lateral force component, properties reminiscent of the dynamics seen in the terrestrial locomotion of sprawled animals. As with terrestrial locomotion, fish may switch gaits in order to move most efficiently at different speeds or to be more maneuverable when locomotion is combined with other behaviors such as feeding and courtship (*38*).

Flying animals also create vortices as they move through the air (Fig. 1, F and G) (*32, 39–41*). Wake visualization has revealed transitions in the pattern of vortex structure with flight speed (*42–44*) that may be loosely analogous with the gait changes in terrestrial (*45, 46*) and aquatic (*38*) animals. Flight is, however, distinct from swimming because, in addition to the thrust required to move forward, a flying animal must generate sufficient lift to remain aloft. Simply explaining how animals generate enough lift poses a substantial problem. For flying insects, conventional steady-state aerodynamic theory cannot explain how wings create forces of sufficient magnitude to keep an animal aloft, especially during hovering flight when lift production is not augmented by the forward velocity of the body (*47*). As with other forms of locomotion, new advances in the understanding of insect flight came from examining the dynamics of force production, revealed through flow visualization (*48*), dynamically scaled model insects (*49–51*), and computational approaches (*52*). At the high angles of attack used by most insects, a conventional airfoil would exhibit stall, the catastrophic loss of lift due to separation of flow from the top surface of the wing. In contrast, an insect wing actually generates enhanced lift at such high angles because of the formation of a large vortex at the leading edge of the wing (*50, 51*). The strength of the vortex and the resultant lift are further enhanced by the rotation of the wing. By properly timing the rotation of a wing as it passes through the wake of a previous stroke, an insect can recapture some of the energy lost to the wake (*51*). This form of energy recovery from one stroke to the next is reminiscent of the elastic storage mechanism described for terrestrial locomotion, but in this case, energy is stored as and recaptured from vorticity within the fluid wake.

The mechanisms of swimming and flying described above are used by microscopic animals. When these very small organisms move through water or air, the viscous resistance of the fluid to being sheared is greater than the inertia that keeps the tiny volume of disturbed fluid moving. For this reason, very small creatures can propel themselves forward by pushing against the viscous resistance of fluid. In the viscous world of microscopic organisms, fluid motions are damped out as soon as an organism stops flapping or undulating, bodies do not coast, and a back-and-forth flap puts you back where you started. A combination of high-speed videography, digital particle image velocimetry, and mathematical modeling is revealing that the force produced when a microscopic structure shears the surrounding viscous fluid depends on various factors, including the structure's orientation, shape, leakiness, or its movement relative to another body. Asymmetries in any of these factors during a cycle of flapping or undulating by a tiny creature can produce motion of the organism relative to the fluid (*53–56*).

An overriding theme of animal locomotion is that propulsive forces vary with time and that the kinetic energy of bodies and limbs may be stored as gravitational potential, strain energy, or fluid velocity for subsequent use. Propulsive forces also vary in orientation, and at any given instant, a locomotor appendage may push an animal orthogonal or even against the direction of motion. Although such variation may reflect unavoidable constraints inherent in the propulsive mechanism, forces generated orthogonal to the direction of motion may also contribute to the overall stability of locomotion. Such control is important because the movements of animals and the natural environments through which they must navigate are complex and variable.

Leaving the Straight and Narrow

Although treadmills, running tracks, flumes, and wind tunnels have been important tools for studying animal locomotion, knowledge of how animals move in the real world and interact physically with their natural environments is also critical to understanding locomotory performance. Several themes are emerging from studies of animals moving through natural environments, now possible because of a variety of technical advances (*1*). First, trade-offs exist between various ecologically important aspects of locomotory behavior. Second, both the mechanical properties of and the forces exerted by the natural environment affect locomotory performance. Third, locomotion in nature is often temporally variable and spatially complex.

Studies of organisms in nature help to identify trade-offs between different aspects of locomotory performance and between locomotion and other important functions. Treadmill or flow tank studies of continuous locomotion often emphasize the energy efficiency of transport, but in many cases, other roles of locomotion, such as predator avoidance or prey capture, can be more important to survival and reproductive success. Identifying the ecological roles of locomotion for diverse organisms helps us decipher the relation between locomotory performance and body design. For example, 40% of the body mass of a shrimp is devoted to the large, tasty abdominal muscles that produce a powerful tail flick during rare, but critical, escape behaviors. During escape, rapid acceleration, rather than energy minimization, is the relevant aspect of performance (*57*). Jellyfish provide an example of a trade-off between locomotion and another important biological function, feeding. Jet propulsion by bullet-shaped jellyfish is more energy efficient than that of dish-shaped jellyfish (*58*), but the vortices produced by dish-shaped animals carry prey to their tentacles more effectively than the vortices produced by bullet-shaped animals (*59*). The recognition of such compromises, which may be quite common in the design of locomotor systems, requires an understanding of the ecology and life history of the species being studied.

A real-world view also reveals that the mechanical properties of the environment through which an animal moves can have profound effects on its performance. For example, not only does the elastic energy storage in the musculoskeletal system determine the dynamics of running (Fig. 1B), but so do the compliance and resilience of the substratum on which they run (*60, 61*). Similarly, the density of the air through which birds and insects fly affects the magnitude of the lift and thrust they can generate, which can explain differences in their flight performance and foraging strategies in habitats at different altitudes (*62, 63*). A more extreme change in fluid density occurs daily for animals that live in the intertidal zone. When intertidal crabs walk or run on the ground above the waterline, gravitational forces predominate and they use a gait similar to that of insects. However, when the tide comes in and the crabs are buoyed up by the water around them, hydrodynamic forces are more important than gravity. Underwater, the animals switch to a gait in which only an occasional push with one or two legs on the substratum is sufficient to keep the animal gliding horizontally (*64*).

Animals moving in the real world are buffeted by dynamic loads imposed on them by the environment. For example, animals living on wave-swept shores are exposed to rapid back-and-forth water flow. The hydrodynamic forces imposed by each wave can overturn a locomoting crab or shear it off the substratum, and the dynamic nature of ambient water flow constrains when and where crabs can walk and run (*65*). Wind and water currents in natural environments are turbulent, so animals swimming, flying, gliding, or running in the real world can be blown off course by brief gusts of rapidly moving water or air. Some body designs are mechanically stable and passively right themselves after

such perturbations. However, such stable designs not only resist externally imposed changes in an organism's trajectory, but they also resist changes imposed by the animal itself. In contrast, mechanically unstable bodies that can easily be blown off course are also very responsive to voluntary steering maneuvers. This trade-off between maneuverability and passive stability can be seen in the designs of some aquatic and terrestrial animals (*66, 67*).

The emerging picture of animal movement in natural habitats is a series of temporally varying and spatially complex paths, rather than constant speed locomotion in straight lines. Analyses of the locomotor patterns actually used by animals in nature have driven important innovations in laboratory investigations of underlying mechanism. For example, field measurements revealed the intermittent nature of crab locomotion. Laboratory studies of crabs using such ecologically relevant behavior led to the discovery that they could travel twice as far before fatiguing if they moved intermittently rather than continuously at the same average work rate (*68*). Because steady locomotion is more the exception than the rule for animals traveling through natural environments, mechanistic studies of animal behavior must consider not only how animals generate locomotory patterns, but also how they control them in both time and space.

Control Systems Are Closely Coupled

Locomotory appendages and body segments not only exert forces on a complex, dynamic external world, but also sense the forces they exert. A suite of neurosensory devices measure the magnitudes and dynamics of force and length changes in the musculoskeletal system throughout each cycle of locomotion (*69*). In addition, viscoelastic behavior of the musculoskeletal system itself provides a form of nonneural feedback that can operate almost without delay. Rapid feedback from both neuronal and mechanical pathways is integrated with guidance from eyes, ears, noses, and equilibrium organs to direct an animal toward a desired locale or stabilize it in the face of an environmental perturbation. The distributed and synergistic nature of feedback is what makes locomotor behaviors so robust.

The process that gives rise to locomotion is not a linear cascade (Fig. 2). Motor output is constantly modified by both neural and mechanical feedback (*70*). Specialized circuits within the nervous system, called central pattern generators (CPGs), produce the rhythmic oscillations that drive motor neurons of limb and body muscles in animals as diverse as leeches, slugs, lampreys, turtles, insects, birds, cats, and rats (*71, 72*). Although CPGs may not require sensory feedback for their basic oscillatory behavior, such feedback is essential in structuring motor patterns as animals move. This influence may be so strong that certain sensory neurons should be viewed not as modulators but as integral members of a distributed pattern-generating network that comprises both central and peripheral neurons (*73, 74*).

Neural feedback from sensors during locomotion takes three general forms (Fig. 2). First, tonic input from directional sensors such as eyes, ears, and noses influences the overall speed and direction of locomotion. Such input is essential in guiding an animal toward a specific destination, avoiding obstacles, attacking prey, or avoiding predators. Second, specialized equilibrium organs such as the inner ears, statocysts, and halteres function to maintain specified body orientation during locomotion. Third, rapid phasic feedback, predominantly from mechanosensory cells, can tune cyclic motor patterns on a cycle-by-cycle basis, either by modulating cells within CPGs or by activating motor circuits that operate in parallel with pattern-generating networks. The muscles and tendons of vertebrates and the external cuticle and muscles of invertebrates are replete with diverse arrays of mechanoreceptors that monitor body kinematics and force production during locomotion. The reason that mechanoreceptors are found in such high numbers is that the properties of cells within a given submodality are not uniform, but differ systematically in their spatial selectivity and temporal response properties. Thus, by integrating information across an array of sensors, a rich blend of information is available for tuning motor output to changes of the internal and external environment within or between locomotor cycles.

Working in parallel with sensory systems, the dynamics of the mechanical system plays a role in providing feedback control from the environment (*13, 75*). The resistance of musculoskeletal structures to being deformed depends on how far they are deformed (elastic properties) and the rate of deformation (viscous properties). Such viscoelastic behavior produces responses to disturbances before the fastest neural reflexes (*76–79*). This preflexive mechanical feedback provides an additional component that functions in parallel with reflexive neural feedback and feedforward control from motor circuits (*80–82*). Mechanical preflexes can reduce the instability associated with high neural reflex gains, slow nerve conduction velocity, synaptic transmission delays, and slow muscle activation kinetics. In addition to properties of musculoskeletal elements, whole appendage and body geometry can play a role in control as well. For example, the sprawled leg posture of the cockroach (Fig. 1C) increases stability in the horizontal plane. Surprisingly, a dynamic model of a cockroach that prescribes leg forces using a feedforward oscillator, analogous to a CPG, self-stabilizes at the animal's preferred speed and rejects artificially imposed perturbations, even in the absence of a neural feedback component (*27*).

The task of integrating the analysis of the sensory and mechanical components of loco-

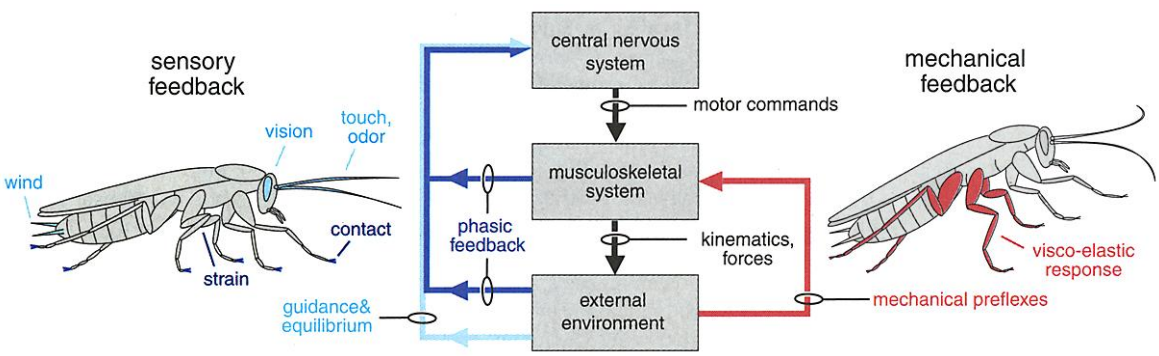

Fig. 2. Both neural and mechanical feedback play roles in controlling locomotion. Although depicted here for a cockroach (shown running slowly on the left, running fast on the right), the diagram represents a general model for locomotor control. The central nervous system generates motor commands that activate the musculoskeletal system of the animal. The musculoskeletal system, in turn, acts on the external environment. The external environment is sensed by multiple modalities and fed back to the central nervous system. Sensory feedback may be divided into three broad categories: guidance and equilibrium from a variety of different modalities (shown combined as light blue) and rapid phasic feedback from mechanosensors (dark blue) (*122*). The nervous system processes the sensory feedback and modifies the motor commands. In parallel, viscoelastic mechanical preflexes (red) act rapidly to resist perturbations.

motor feedback appears daunting at first. With multiple joints distributed throughout animals' bodies and appendages, each serviced by two or more muscles, animal movement involves many degrees of freedom. However, musculoskeletal systems can be more easily understood by identifying groups of muscles, joints, and appendages that act in concert as if they were one single element. Such synergistic assemblages may be incorporated into simple models or templates that identify a reduced number of control targets (*83*). An example of just such a template is shown in Fig. 1B. Two-, four-, six-, and eight-legged animals can be represented by a single virtual leg spring because one human leg works like two legs of a trotting dog, two legs of a trotting lizard, three legs of an insect, and four legs of a crab (*84*). The next step is to anchor such simple templates in more realistic models with muscles and joints that will allow testing of particular hypotheses of neural control involving reflexes and motor circuits.

Sensory feedback reflexes and mechanical preflexes are complimentary pathways that provide feedback from the environment. Future studies of motor control should address the dynamic coupling among CPGs, sensory feedback, mechanical preflexes, and the environment. Such integration promises to provide a global view of motor control and will likely redefine the roles of the individual components. For example, the output of motor neurons can only be decoded by considering the mechanical properties of the musculoskeletal system. Similarly, it is difficult to correctly interpret the biomechanical design of the musculoskeletal system without considering its associated sensory-motor circuitry. Neural signals are not commands but are suggestions sent to a mechanical system possessing its own behavior realized through its physical interaction with the environment (*85, 86*). Because neural and mechanical systems are dynamically coupled to each other and to the environment, it is not always clear what exactly is being controlled and where the control originates (*87*). Ultimately, however, the voluntary changes in locomotion originate in higher centers of the brain that are under the influence of the visual, olfactory, auditory, or other sensory systems used in guidance. The means by which this descending input influences motor patterns must be viewed within the context of a highly interconnected system. For example, to accomplish a voluntary change in motion, descending commands could temporarily override local stability reflexes. Alternatively, descending commands could simply manipulate the gain of local reflexes, thereby manipulating a neural-mechanical feedback system to produce a controlled response (*88–90*). Evidence that higher centers can alter local feedback circuits is seen in the flight system of flies (*91–93*), in which descending visual input activates muscles that control the position of the animal's head and the motion of the haltere, an organ that serves as the gyroscope. As described in the next section, our understanding of how muscles drive and control the body and limbs has become increasingly sophisticated and more realistic.

Muscles Are More Than Motors

Paralleling recent research on whole-organism locomotion in natural environments, studies at the muscle level have provided the first glimpses into how muscles actually function in moving animals. Research on isolated muscle under controlled conditions continues to define what muscles can do, but the integration with whole-animal mechanics has substantially expanded the known range of muscle performance. Studies using single contractions with constant loads and velocities, as pioneered by A. V. Hill, continue to advance our understanding by revealing time-dependent effects of force production (*94*). In locomoting animals, however, the timing and intensity of neural stimulation, muscle length and velocity, as well as intrinsically generated and externally imposed forces may change within a cycle of movement. Over the past 15 years, the development of the work-loop technique has revealed a great deal about muscle behavior under more realistic conditions (Fig. 3) (*95*). This technique uses cyclic oscillation of muscle length and stimulation to simulate natural kinematics and activation, making it possible to quantify the biomechanical consequences of the variation in neural and mechanical input. Work-loop experiments have provided insight into how muscles function as motors that generate force while shortening, and thus produce positive power (Fig. 3, A and B). But work-loop experiments have identified additional roles that muscles play in moving animals. For example, because of large imposed strains, a leg extensor muscle in the cockroach, although capable of power production, actually acts as a brake during running to slow the swing of the leg (Fig. 3C) (*96*). Similarly, control muscles of flies generate little or no mechanical power yet act as controllable springs to direct the forces of much larger power muscles, thus providing the means by which the nervous system can rapidly alter wing kinematics by varying the timing of activation (Fig. 3D) (*97–99*). Such divisions of labor are probably common. Whereas the large pectoralis muscle of a bird powers flight (Fig. 3B) (*100*), another controls joint stiffness and may modulate wing shape during takeoffs and turns (*101*). In general, the timing of activation, which is not even an experimental parameter in isometric or isotonic studies, emerges as an important variable by which the nervous system can regulate mechanical performance. In fish, for example, axial muscle may play either a force-generating or a force-transmitting role, depending on when it is activated with respect to the undulatory wave that passes along the body (*102, 103*). In fish that generate the bulk of their hydrodynamic forces with their tail fin, anterior muscles generate power, which is transmitted to the fin in part through the stiffening action of more posterior muscles (Fig. 3E) (*104*). In eels and other sinuous swimmers, muscles all along the trunk may contribute to the generation of mechanical power (*102*). Like the fly, some fish may regulate the function of their muscles during changes in swimming speed by altering the timing of activation at different regions along their body length (*102, 103*).

Given an ever-broadening view of what muscle is capable of, we can ask what muscles actually do in nature. Estimates of muscle and tendon length changes from anatomy and limb kinematics have been supplemented with direct measurements in locomoting animals using sonomicrometry, which exploits the speed of sound to measure the dynamic length changes (*100, 105–108*). At a finer scale, sarcomere lengths have been measured in swimming fish with laser diffraction (*109*). In addition to providing critical data for work-loop experiments, direct measurements of muscle length have revealed that the kinematics of individual muscle fibers in locomoting animals are not always the same as the kinematics of the muscle-tendon system as a whole. In running turkeys (*106*) and hopping wallabies (*110*), for example, muscle fibers are nearly isometric or even shortening while the tendon stretches (Fig. 3F). Under these conditions, muscles act as struts, permitting the elastic tendons to store and release energy. In a few instances, it has been possible to measure not only the length of muscle in a moving animal, but also the forces it produces or absorbs. Researchers have affixed tiny strain gauges onto tendons (*106*) and have even directly bonded transducers to the wing bones of flying birds (*111*). By measuring both the length and force of a muscle in an active animal, it is possible to calculate in vivo work loops, further broadening our view of how animals produce and regulate power during locomotion. In vivo force measurements are critical because kinematics and anatomy cannot always predict force and power output. Leaping frogs, for example, produce eight times the power than would

be estimated from their muscle length and cross-sectional area (*112–114*). Even for swimming scallops, a simple locomotor system involving one joint and a single power muscle (Fig. 3A), comparison of in vitro and in vivo muscle performance is complicated by hydrodynamic effects and remains controversial (*108, 115, 116*). Given advances in transducer technology, the number of preparations in which it is possible to measure in vivo work loops should increase in coming years, expanding even further our understanding of muscle's diverse roles in locomotion.

Prospective

Integrative and comparative approaches have identified several general principles of animal locomotion, which surprisingly, apply to swimming, flying, and running. The way in which animals exert forces on the external world often allows mechanical energy from one locomotor cycle to be stored and recovered for use in another. The generality of energy-storage mechanisms in different modes of locomotion is just beginning to be explored. Forces lateral to the direction of movement are often larger than one might expect for efficient locomotion, but they may enhance stability, and their modulation is essential for active maneuvers. Mechanisms of nonsteady locomotion, including starting, stopping, and turning, are emerging areas of interest. Technological advances have enabled the nascent studies of locomotion in natural environments and the mechanical interactions of organisms with their environment. Animals use their musculoskeletal systems for a variety of behaviors and, as a consequence, are not necessarily optimized for locomotion. In nature, unlike in the laboratory, straight-line, steady-speed locomotion is the exception rather than the rule. Further, environmental forces make extreme demands on the musculoskeletal system of some locomoting animals. The control system that enables animals to actively steer in the face of these changing conditions combines both neural and mechanical feedback with feedforward control and pattern-generating circuits. The interface between these modes of control offers a rich area for exploration. Finally, methods adapted from muscle physiology, combined with measurements of locomotor mechanics, have revealed many mechanical functions of muscle during locomotion.

The many recent advances in the study of molecular motors are just beginning to be integrated into an understanding of locomotion at the cellular scale. Molecular biology and genetic engineering techniques, such as site-directed mutagenesis, are already being used to link the structure of individual molecules to locomotor performance at the organismal level (*117, 118*). With a more thorough understanding of muscle function, systems-level control, interactions with the environment, and energy transfer acting at the organismal level, locomotor biomechanics is now poised to

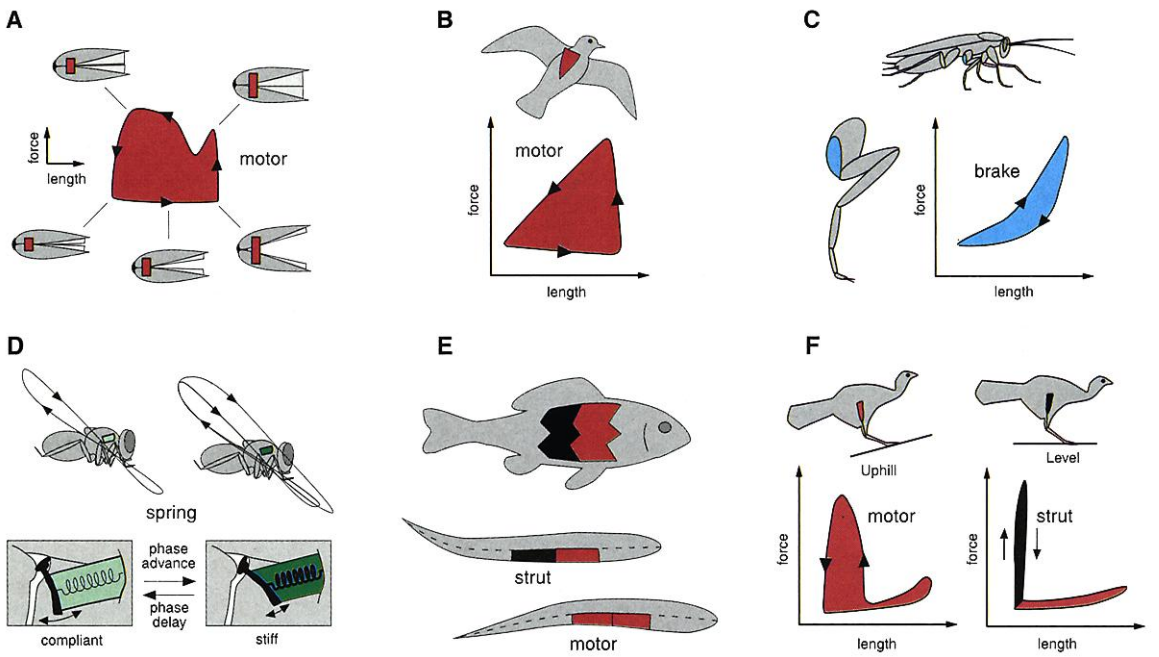

Fig. 3. Muscles can act as motors, brakes, springs, and struts. Muscles that generate positive power (motors) during locomotion and the area within associated work loops are indicated in red. Muscles that absorb power during locomotion (brakes) and the area within associated work loops are indicated in blue. Muscles that act as springs of variable stiffness are indicated in green. Muscles that act to transmit the forces (struts) are shown in black. (**A**) Scallop swimming provides a simple example of a muscle generating positive work to act as a motor. The cycle begins in the lower right corner of the loop, when the gape of the shell is maximal. Activation of the muscle (indicated in the scallop by the red rectangle) causes a rise in force and subsequent shortening producing the pressure to drive a jet of water that propels the animal. At the upper left, the muscle begins to deactivate, force declines, and shortening continues. In the lower left, the muscle is fully deactivated and force is minimal. Along the lower border of the loop, the shells are opened by passive recoil of elastic hinge ligaments. The area enclosed within the loop is equal to the work done (product of force and length change) by the muscle during each cycle. The counterclockwise work loop and red color indicate that the muscle generates positive power during locomotion. Adapted from (*108*) with permission from Company of Biologists Ltd. (**B**) The pectoralis muscle of birds generates the positive power required to fly. In pigeons, it has been possible to measure in vivo work loops with strain gages bonded to bones near the muscle attachment point (force) and sonomicrometric crystals implanted at the ends of muscle fibers (length). Adapted from (*100*) with permission from Company of Biologists Ltd. (**C**) In running cockroaches, some muscles that anatomically appear to be suited for shortening and producing power instead act as brakes and absorb energy because of their large strains. Adapted from (*96*) with permission from Company of Biologists Ltd. (**D**) In flies, an intrinsic wing muscle acts to steer and direct the power produced by the primary flight muscles. Changes in activation phase alter the dynamic stiffness of the muscle and produce alterations in wing motion. Adapted from figure 11 of "The control of wing kinematics by two steering muscles of the blowfly (*Calliphora vicina*)" (*98*), copyright Springer-Verlag. (**E**) In swimming fish, the function of muscles varies within a tail-beat cycle and has been investigated with a variety of techniques in a diversity of species. In some fish designs, early in a beat, the cranial muscle fibers shorten and produce power, which is transmitted by more caudal muscle fibers acting as struts. As the beat continues, the fibers that were previously acting as struts change their role to power-producing motors. The cartoon at the top shows a fish from the side. Beneath it are views from above the fish at two points in the tail-beat cycle. Adapted from (*123*) with permission from Company of Biologists Ltd. (**F**) In vivo muscle force and length measurements in running turkeys indicate a dual role for the gastrocnemius muscle. It generates positive power during uphill running but acts as a strut during level running, which allows the springlike tendons to store and recover energy. Adapted from (*106*).

integrate further across levels of organization from molecules to ecosystems (*119*).

References and Notes

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